

Fruiting and Sporulation of Inland Spruce Cone Rust (*Chrysomyxa pirolata* Wint.) on Bells Wintergreen (*Orthilia secunda* [L.] House) in Relation to Environmental Factors in Northern Finland

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Kaitera, J. and Tillman-Sutela, E. 2015. Fruiting and Sporulation of Inland Spruce Cone Rust (*Chrysomyxa pirolata* Wint.) on Bells Wintergreen [*Orthilia secunda* (L.) House] in Relation to Environmental Factors in Northern Finland. *Baltic Forestry*. 21(1): 38–43.

Abstract

Fruiting and sporulation of *Chrysomyxa pirolata* Wint. were investigated on *Orthilia secunda* [(L.) House] in northern Finland during 2009–2012. Each year of the study, overwintered leaves of *O. secunda* bearing undifferentiated fruitbodies, uredinia, telia or basidia were collected on 5–7 weekly occasions during the early summer (May–June) and local rainfall and temperature sum were registered. Uredinia developed consistently but telia varied in abundance among years of the study period. Undifferentiated fruitbodies began developing in early May regardless of weather conditions. Uredinia development rate and sporulation increased along rising temperature and rainfall during the latter half of May. Telia and basidia developed between late May and mid-June, and ruptured between mid- and late May. Intense periods of rainfall (i.e., >10 mm per day) in late May coincided with formation of telia and basidia provided that the temperature sum exceeded 100 d.d. Telia did not develop when cumulative rainfall was <150 mm. After high abundance of telia and basidia, these rust stages were scarce or lacking in the next year as indication of periodical cycling during the fruiting and life cycle of the rust. Irrespective of temperature sum, fruiting activity during periods of low rainfall in May was limited to the development of uredinia.

Key words: *Chrysomyxa pirolata*, fruiting, inland spruce cone rust, *Picea abies*, sporulation, light microscopy

Introduction

Inland spruce cone rust (*Chrysomyxa pirolata* Wint.) is a significant cone pathogen of *Picea* sp. in northern Europe and North America (Liro 1908, Jørstad 1925, Savile 1950, Ziller 1974, Tillman-Sutela et al. 2004). The rust occasionally causes severe damage to spruce cones in seed orchards (Sutherland et al. 1984, Summers et al. 1986, Singh and Carew 1990). *Chrysomyxa pirolata* is typical heteroecious rust, in which development and sporulation are regulated by environmental factors such as available moisture (Crane and Hiratsuka 2000). The rust forms spermogonia and aecia in cone scales from where it releases airborne aeciospores. On alternate host leaves, *C. pirolata* forms uredinia and telia where basidia with basidiospores develop after germination and spread the rust to pistillate cones (Gäumann 1959, Ziller 1974). The alternate hosts of *C. pirolata* are species of *Pyrola*, *Moneses* and *Orthilia* (Savile 1950, Gäumann 1959, Sutherland et al. 1984). The rust

has frequently affected the seed crop of *Picea abies* (L.) Karst. in Finland (Kangas 1940, Rummukainen 1960, Nikula and Jalkanen 1990). The latest rust epidemics occurred in 2000 and 2006 during abundant seed years when Cherry spruce rust (*Thekopsora areolata* [Fr.] Magnus) was the main pathogen affecting the seed crop (Savonen 2001, Kaitera et al. 2009a) although *C. pirolata* was also involved.

The aim of this study was to investigate the variation in fruitbody formation and sporulation of *C. pirolata* on sidebells wintergreen (*Orthilia secunda* [L.] House), one of its known alternate hosts in northern Europe, in relation to rainfall and temperature.

Materials and Methods

Overwintered leaves of *O. secunda* infected by *C. pirolata* were collected in Muhos (64°48'N, 26°00'E), northern Finland, on a weekly basis during the early summer (May–June) from 2009 to 2012. Seasonal fruit-

ing and sporulation of cone rusts (incl. *C. pirolata*) has previously been investigated in cones and alternate hosts in the same location from 2006 to 2008 (Kaitera et al. 2009a, b). The study area was a moist, nutrient-rich site containing mature Norway spruce [*Picea abies* (L.) Karst.]. A sample of 9-46 infected leaves of *O. secunda* was collected on 5-7 separate occasions each year during the study period 2009-2012 (Table 2). The area (%) covered by each fruiting stage was estimated for lower leaf surface using a stereomicroscope. Fruiting stages are illustrated with stereo microscope (SM) and field emission scanning electron microscope (FES-EM) images: undifferentiated immature fruiting structures characteristic of *C. pirolata* (Figures 1 and 3), uredinia (Figures 1 and 4), telia and basidia (Figures 2 and 5). Detailed descriptions of these stages and spores are provided in Gäumann (1959), Crane and Hiratsuka (2000), Crane (2001), and Kaitera et al. (2009a). In addition, coverage of fruiting stages visible below the leaf surfaces was recorded. The state of sporulation (i.e., active/complete/rupturing) was also recorded for uredinia and telia.

Daily rainfall and temperature sum (threshold value of 5 °C) data were obtained from the Finnish Meteorological Institute (Venäläinen et al. 2005) for a location (lat. 7185000, long. 3455000) adjacent to the study site. Data of dew was not available from the location. Cumulative rainfall before the rust fruiting (January-April) includes also snow. Variation in these parameters was compared to leaf area covered by each fruiting stage during the study period (May-June) in each year from 2009 to 2012. The variations in rust fruiting are presented together with cumulative parameters in Table 2 and also with daily rainfall graphically (Figures 6-13).

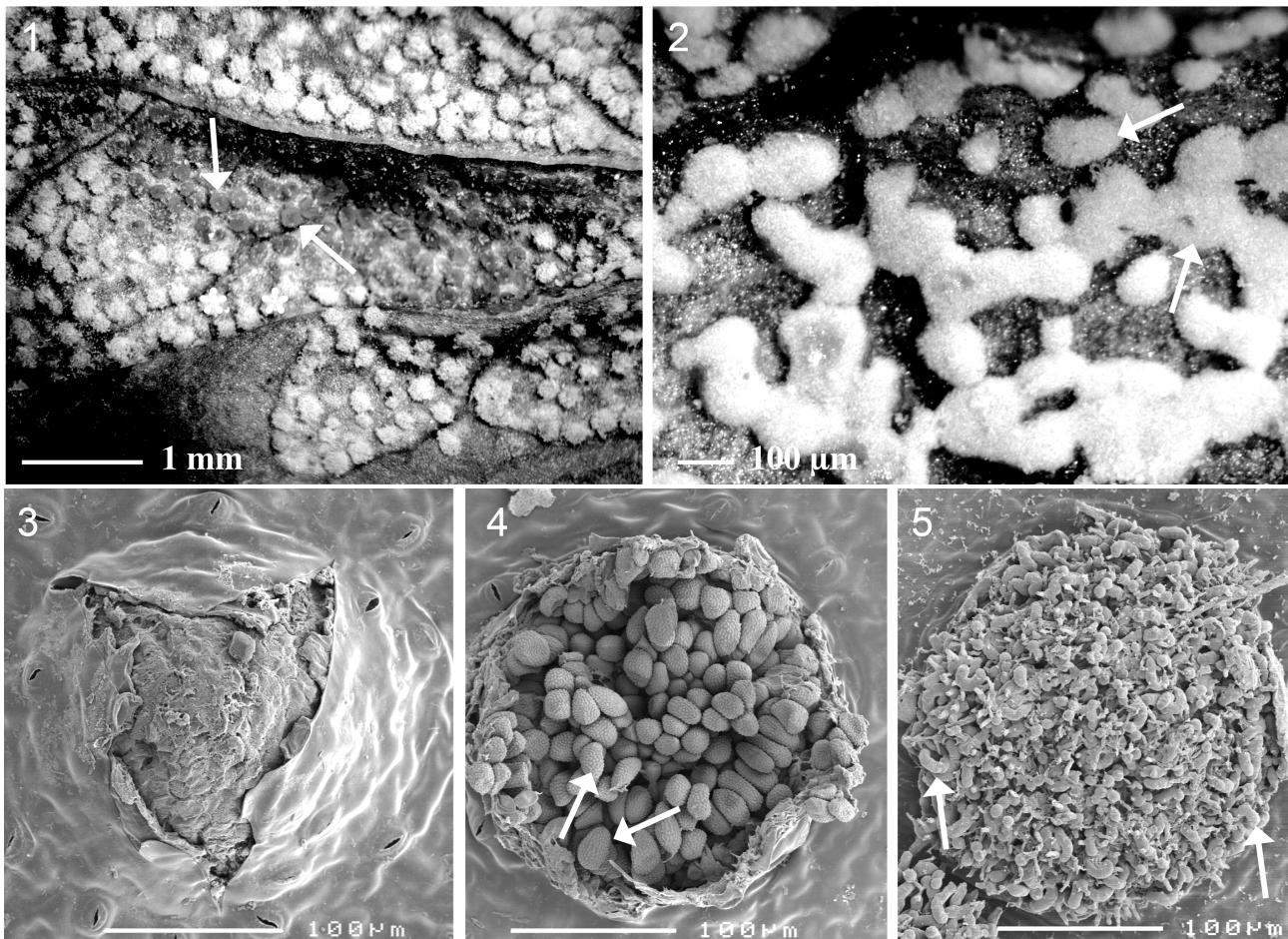
In the study site, the cone crop was abundant in 2006 and moderate in 2012, while only a few trees developed a good number of fresh cones in 2007 and 2010 (Table 1). Fresh cones were either very rare or lacking in 2008, 2009 and 2011. From 2006 to 2011, the frequency of randomly sampled cones with *C. pirolata* aecia was 7% in 2006 (Kaitera et al. 2009a) and 2007 (Kaitera et al. 2009b), 0% in 2008, 2009 and 2011, and 6% in 2010 (Kaitera and Tillman-Sutela 2014). In 2012,

Table 1. General annual frequency of cone crop in the study area and percentage of cones infected with *Chrysomyxa pirolata* in previous collections (see the text for references)

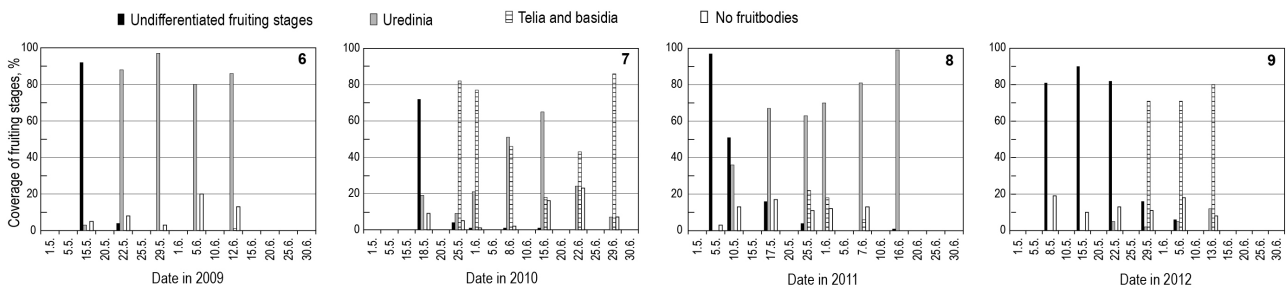
Cones	Year						
	2006	2007	2008	2009	2010	2011	2012
Frequency of cone crop	Abundant	A few	Rare	Rare	A few	Rare	Moderate
Cones bearing <i>C. pirolata</i> fruiting stages	7%	7%	0%	0%	6%	0%	26%

Table 2. Weekly fruiting of *C. pirolata* on *Orthilia secunda* in Muhos 2009-2012. Cumulative temperature sum (threshold value of 5 °C) and rainfall were compiled from 1 January to the sampling period and to the time (30 April) before the fruiting observations started

Year	Date	Leaves	Leaf coverage (%) by fruiting stages of <i>C. pirolata</i>										T°	Rain-fall	
			Undifferentiated		Uredinia		Telia		Basidia		Immature stages below surface				
			N	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean			Std
2009	1.1.-30.4.													7	100
	15.5.	30	76	30	2.6	11	0	-	0	-	16.0	27.0	44	126	
	22.5.	38	3	12	88	18	0	-	0	-	1.1	3.7	84	130	
	29.5.	9	0	-	97	5	0	-	0	-	0	-	131	142	
	5.6.	46	0	-	80	20	0	-	0	-	0.1	0.7	179	143	
	12.6.	27	0	-	86	16	0.7	3.8	0	-	0	-	217	151	
2010	1.1.-30.4.													2	182
	18.5.	42	70	34	19	30	0	-	0	-	1.7	3.5	101	190	
	25.5.	26	2.5	11	9	11	82	20	68	40	0.9	1.6	167	204	
	1.6.	33	0	-	21	36	77	37	77	37	1.1	1.7	205	212	
	8.6.	24	0	-	51	40	46	41	46	41	0.5	1.5	234	236	
	15.6.	30	0	-	65	35	18	27	18	27	1.0	2.3	278	248	
	22.6.	14	0	-	24	34	43	34	43	34	0	-	334	253	
	29.6.	18	0	-	7	9	86	25	86	25	0	-	400	262	
2011	1.1.-30.4.													12	120
	5.5.	23	95	6	0	-	0	-	0	-	1.5	2.0	12	120	
	10.5.	27	42	31	36	34	0	-	0	-	8.5	11.4	30	120	
	17.5.	16	15	25	67	33	0	-	0	-	1.1	1.3	58	142	
	25.5.	37	3	14	63	35	22	28	0	-	0.7	1.1	105	159	
	1.6.	27	0	-	70	29	18	15	14	28	0.3	1.0	152	180	
	7.6.	17	0.1	0.2	81	18	6	-	6	15	0.1	0.5	208	181	
	16.6.	9	0	-	99	2	0	-	0	-	0.6	1.7	320	186	
2012	1.1.-30.4.													4	136
	8.5.	27	63	25	0	-	0	-	0	-	17.9	17.0	5	144	
	15.5.	28	88	17	0	-	0	-	0	-	2.1	2.3	23	175	
	22.5.	37	82	23	5	9	0	-	0	-	0.4	0.5	60	200	
	29.5.	40	16	14	2	2	71	20	40	39	0.1	0.3	103	200	
	5.6.	32	6	19	5	10	71	27	71	27	0	-	129	223	
	13.6.	17	0	-	12	22	80	30	80	30	0	-	179	231	



Figures 1-5. SM and FESEM images of fruiting stages of *Chrysomyxa pirolata* on leaves of *Orthilia secunda*. 1. Undifferentiated fruiting stages (arrow) and uredinia (star). 2. Telia and basidia (arrow). 3. An undifferentiated fruiting structure. 4. A sporulating uredium with urediniospores (arrow). 5. A mature telium with germinating basidia (arrow) and basidiospores



Figures 6-9. Annual average coverage (%) of undifferentiated fruiting stages (incl. immature fruiting stages below the leaf surface), uredinia, telia and basidia of *Chrysomyxa pirolata*, and coverage without fruitbodies (no fruitbodies) on leaves of *Orthilia secunda* collected in Muhos, northern Finland during May-June. 6. Year 2009. 7. Year 2010. 8. Year 2011. 9. Year 2012

26% of fresh cones collected in early July bore rust spermogonia or aecia (unpublished data).

Results

Variation in fruiting and sporulation of C. pirolata

Undifferentiated fruitbodies were the first to appear and most common type of fruiting structures (coverage max. 70–95% per annum, Table 2, Figures 6–9) on overwintered leaves of *O. secunda* in the first half of May during the study period 2009-2012. Immature fruiting stages were also detected below the underside of leaf

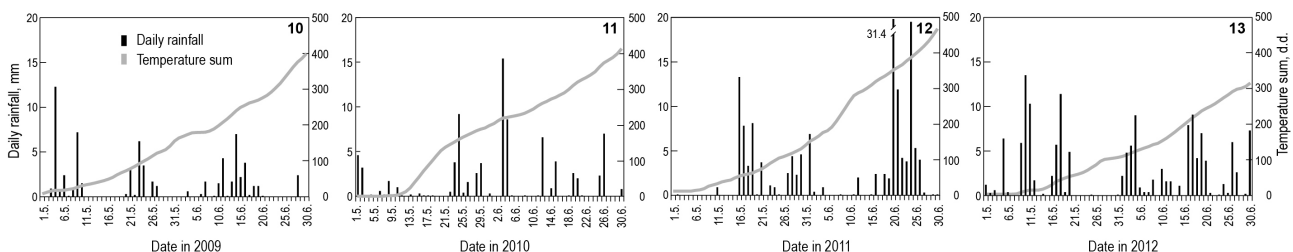
surfaces at low abundances (2–18%: Table 2). The occurrence of undifferentiated fruiting stages decreased rapidly in late May, although small patches could still be found in early June. Development of undifferentiated fruitbodies into uredinia always began between the first and the last week of May. In 2009, uredinia reached the peak coverage of 97% between late May and mid-June. Few telia or basidia were detected on leaf surfaces in May–June. In 2010, occurrence and coverage of uredinia was more variable (9–65%) on leaves between mid-May and mid-June (Figure 7). Later in 2010, telia and basidia were common and abundant (18–86% coverage) from late May and throughout June. In 2011, uredinia were the most frequently observed fruiting stage with the peak of 99% coverage from early May to mid-June (Figure 8). Telia and basidia developed with low abundance (6–22%) on leaves of *O. secunda* between late May and early June. In 2012, uredinia were rare covering from 2–12% of leaf surfaces between the late May and mid-June (Figure 9). At the same time, telia and basidia formation was high and these stages covered 71–80% of leaf surfaces.

The onset of sporulation of urediniospores varied among years, beginning in early May of 2011, mid-May of 2009, late May of 2012, and in early June of 2010. Sporulation was complete by early June of 2009 and 2011, and by late June of 2010. Telia with basidia began rupturing in early June in 2010, and in mid-June of 2011 and 2012.

wet periods occurred with ca. 16 mm (in 21–27 May) and 8 mm (7–11 June) of rain (Figure 10). Monthly rainfall was 42 mm in May 2009 (1961–2013 average: 37 mm) and 28 mm in June (average: 50 mm). In 2010, cumulative rainfall was very high, exceeding 200 mm by the end of May. Total rainfall was ca. 57 mm between mid-May and mid-June, during which wet periods occurred with ca. 21 mm (23–29 May), 24 mm (3–4 June), 11 mm (12–15 June) and 5 mm (19–20 June) of rain (Figure 11). Monthly rainfall was 35 mm in May and 51 mm in June. In 2011, cumulative rainfall was ca. 65 mm between mid-May and mid-June. Wet periods with ca. 36 mm (16–21 May) and ca. 21 mm (27 May–1 June) occurred during that time (Figure 12). Monthly rainfall was 53 mm in May and 98 mm in June. In 2012, rainfall was high in early May and increased from late May until early June. Between early May and mid-June, total rainfall exceeded 88 mm and wet periods occurred with ca. 31 mm (9–12 May), 25 mm (16–20 May) and 22 mm (1–4 June) of rain (Figure 13). Monthly rainfall was 65 mm in May and 83 mm in June.

Rust fruiting in relation to precipitation and temperature

In 2009, the driest period coincided with abundant production of uredinia and a lack of telia in May–June (Figures 6 and 10). During this period, very few telia developed on leaf surfaces. Temperature sum was <100 d.d. before late May (Table 2) and uredinia formation



Figures 10–13. Variation in daily rainfall (mm) and temperature sum (d.d.) between 1 May and 30 June in Muhos, northern Finland. 10. Year 2009. 11. Year 2010. 12. Year 2011. 13. Year 2012

Daily rainfall and temperature sum during the study period

Daily rainfall and temperature sum varied greatly within and among years of the study period (Table 2, Figures 10–13). Temperature sum remained 20–50 d.d. until mid-May in 2009 (Figure 10), 2011 (Figure 12) and 2012 (Figure 13), while it exceeded ca. 100 d.d. in 2010 by this date (Figure 11). At the end of May, the temperature sum exceeded 200 d.d. in 2010 while it remained < 150 d.d. in other years.

In 2009, cumulative rainfall was low during May and early June (Table 2). Total rainfall was ca. 25 mm between mid-May and mid-June. During that time, two

remained low. The few rainy days in late May coincided with an increase in the formation of uredinia but not telia. The end of May and early June were dry. Although telia and basidia were lacking during this period, the rust multiplied and spread efficiently among alternate hosts but not to pistillate cones. In 2010, the early summer (late May to late June) was wet and telia were abundant (Figures 7 and 11). Temperature sum rapidly increased to over 100 d.d. in mid-May (Table 2), coinciding with moderate formation of uredinia. The rust enjoyed a moderate spread among alternate hosts via urediniospores in 2010, and dissemination of basidiospores to spruce cones was high. In 2011, ured-

inia formation peaked during a wet period between mid-May and mid-June along increasing temperature sum (Figures 8 and 12). Telia developed with low frequency, however, only between late May and early June, coinciding with a period of high rainfall at the end of May. The rust spread efficiently among alternate hosts in 2011, but infection of spruce cones via basidiospores was low. In 2012, few uredinia were formed during May–June (Figure 9). May was very cold, and the temperature sum remained below 100 d.d. until the end of the month (Table 2, Figure 13). In early May, wet periods did not affect uredinia formation but rain in late May and early June was associated with an increase in telia and basidia. Spread of the rust among alternate hosts by urediniospores was probably minimal, while infection of spruce cones via basidiospores was high.

Discussion

In this study, the earliest and the most abundant fruiting stages of *C. pirolata* on overwintered leaves of *O. secunda* were undifferentiated fruitbodies in early May. Fruiting observed in the present study was similar to that described in southern and northern Finland by Kaitera et al. (2009a). Immature stages developed first into uredinia and then, depending mainly on rainfall, into telia and basidia. This agrees with earlier reports of fruiting in *C. pirolata* (Summers et al. 1986, Kaitera et al. 2009a). Earlier, Crane and Hiratsuka (2000) showed experimentally how undifferentiated young uredinia develop into telia under wet conditions while older uredinia do not convert in a similar way even when thoroughly wetted. This appeared to be the case for our 2011 observations. Our 2009 data are consistent with Kaitera et al. (2009a), in that very dry weather may prevent formation of telia and basidia. Rainfall is known to affect telia formation and basidiospore release on *Picea mariana* (Mill.) Britton, Sterns & Poggenburg (Singh and Carew 1990).

In addition to rainfall, we observed that temperature sum is important to the fruiting process, especially in May. Uredinia were typically scarce or absent, when the temperature sum was below 100 d.d. in early May of 2009, 2010 and 2012. However, uredinia developed under a lower temperature sum in 2011, when the rainfall was abundant. Telia were also lacking at temperature sums less than 100 d.d. The rate of telia formation in *C. pirolata* is directly related to temperature (Crane and Hiratsuka 2000). Our observations concerning the formation, sporulation and rupture of uredinia, telia and basidia during May–June agree with earlier reports of fruiting and sporulation of this rust in Finland (Kaitera et al. 2009a).

During the study period, *C. pirolata* sporulated with uredinia strongly in 2009 and 2011, moderately in 2010 and scarcely in 2012. Therefore, some periodical cycling was observed in fruiting and sporulation rates within hosts but at no point was the rust life cycle interrupted. Similarly, telia formation showed a periodicity in that telia were abundant in 2010 and 2012, scarce in 2011, and absent in 2009. Low telia abundance translates into reduced infection of spruce cones and less damage to the seed crop. Telia formation appears to depend on the coincidence of rust life cycle and adequate rainfall and minimum temperature sum of 100 dd. Cases when these factors do not coincide have been discussed by Rummukainen (1960). In the study area, good-to-abundant cone crops in 2006, 2007 and 2012 coincided with high telia formation following greater-than-average rainfall during May. In addition, a good cone crop with typical May rainfall occurred in 2010. Despite of frequent formation of telia and basidia on alternate hosts in 2007, 2010 and 2012, the conditions for a high *C. pirolata* incidence in cones occurred only in 2012, when periodicity and frequency of rust fruiting and sporulation, environmental factors, and frequency and progress of pistillate cones were optimal at the same time.

Acknowledgements

We thank Mrs. Irene Murtovaara for preparing the figures and Dr. Michael Hardman for checking the language.

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Received 13 November 2014
Accepted 29 January 2015